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Effects of barriers on functional connectivity of riparian plant habitats under climate change

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ABSTRACT

Alterations of riparian areas of running waters resulted in fragmentation of the riverscape. The possible impact of climate change additionally stresses the importance for conservation planning for riparian habitats, especially for sessile plant species. The survival of species under changing habitat availability can be counteracted by ensuring functional connectivity of riparian plant species. This study applies a coupled modelling framework using species distribution models and dispersal simulations, which allow to analyze the potential future distribution of species in relation to their ecological niche, life history traits including dispersal abilities as well as barriers to dispersal such as dams. Modelled suitable habitats for six riparian plant species characteristic for the olive willow plant community (*Salicion elaeagni*) showed dramatic changes under the impact of two climate change scenarios. While habitat suitability remained low for species with a narrow ecological niche, it increased under climate change scenarios for species which are also found in secondary habitat outside riparian areas. Simulations of dispersal to the potential future habitat revealed nevertheless high numbers of decolonized cells after 80 years of dispersal for species with high future habitat suitability. This stresses the importance of a joint investigation of the habitat suitability under climate change scenarios, dispersal parameters as well as life history traits for conservation planning of riparian species. The simulated future distribution revealed that barriers along rivers have a significant negative effect on the spread of the studied plant species. Our results suggest that conservation management should focus on providing connected stepping stone habitats for riparian plant species along rivers, as current species occurrences are not persistent over time.

1. Introduction

Conservation of riparian areas is crucial, as its azonal vegetation shows high species diversity and also a different species composition from zonal adjacent areas (Catford and Jansson, 2014; Sabo et al., 2005). River alterations due to e.g. hydropower or agricultural land requirements decrease habitat availability for floodplain ecosystems (Lytle and Poff, 2004). The decline of riparian areas along rivers has to be avoided, as they can mitigate flooding damage in e.g. nearby agricultural landscape (Darby and Sear, 2008). Additionally, riparian vegetation prevents erosion of river banks (Darby and Sear, 2008). The fragmentation of the riverscape, resulting in local habitat of lower quality disrupting species exchange (see Haslam, 2008), can be counteracted by ensuring functional connectivity of riparian species (Davis et al., 2013).

The ability to disperse in a certain landscape (functional connectivity) is highly species specific (Vogt et al., 2009). Structural elements such as stepping stone habitats, providing sufficient space for the temporal survival of small populations, are crucial to link larger populations or metapopulations, if space for riparian habitats is limited (Freckleton and Watkinson, 2002). They ensure gene flow between populations of a species, as well as recolonization of habitats after extreme events like e.g. floods (Mari et al., 2014). In highly fragmented landscapes, stepping stones are even crucial for mobile species such as birds (Saura et al., 2014).

Sessile riparian plants show adaptation to fluctuating water availability, flood occurrence as well as drought and are thus highly adapted to environmental changes (Ellenberg, 2010). The ability to spread by vegetative reproduction as well as multiple vectors for dispersal (polychory) ensures the survival of plant species (Schnurr et al., 2010). Especially water-mediated dispersal (hydrochory) is considered a major driver of riparian species biodiversity (Konar et al., 2013), but is mainly acting in a linear manner downstream (Nilsson et al., 2010). Regulated rivers as well as barriers such as dams can prevent the successful spread of a species downstream (Jansson et al., 2005; Werth et al., 2014). Therefore, upstream seed dispersal by wind or animals is crucial for

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plant species, especially for functional connectivity along and between river catchments (Werth and Scheidegger, 2014; Wubs et al., 2016).

Knowledge on dispersal vectors and dispersal distances in general and specifically of riparian species is still rare (e.g. see Wubs et al., 2016), although they are highly important for conservation and therefore revitalization planning (Driscoll et al., 2014; Pullin et al., 2009). Given the high fragmentation of current riverscapes, dispersal to suitable habitat becomes less likely due to e.g. barriers and land use change (Alldredge and Moore, 2014; Brown and Chenoweth, 2008; Jansson et al., 2000; Sitzia et al., 2016; Werth et al., 2014). Dispersal of riparian plants is highly affected by human-made barriers, such as dams and dykes (Mosner et al., 2012; Pollux et al., 2007; Werth et al., 2014). These barriers are not only limiting water-mediated dispersal, but can also be detrimental for wind-dispersed seeds. Backwater, limited flow velocity (up to almost still water conditions) as well as lack of river dynamics all result in unreachable habitat up- and downstream of barriers which can only be crossed by rare long-distance dispersal (e.g. by strong winds or floods). Still, artificial barriers are not necessarily static and could be altered (Caplat et al., 2016), but planning for modifications requires a joint investigation of the impact of both barriers and dispersal abilities for the spread of riparian plant species.

The spread of populations of a species is also influenced by habitat alterations or loss due to land use and climate change (see Brook et al., 2008). The future distribution under climate change scenarios predict a decrease of habitat for riparian plant species (Ikeda et al., 2014) and a reduction in species richness due to increased summer droughts and increased winter flooding (Garssen et al., 2017; Garssen et al., 2014). For conservation planning in riparian areas, habitat key characteristics need to be determined, adding additional complexity as floodplains consist of a highly dynamic habitat mosaic (Naiman et al., 2005). Therefore, studies aiming at detecting suitable areas for river restoration mainly use information on characteristics linked to rivers (e.g. flow regime, wetness index, see Anderson et al., 2011), which are less dynamic. Predictions taking into account climate change and habitat key characteristics are still rare.

Commonly used species distribution models (SDM, alternatively “niche modelling”) have proven to been valuable for conservation decisions in general (Guisan et al., 2013; Reichert et al., 2007), allowed to model rare species (Breiner et al., 2015), and some methods have also been applied to river networks (see Elith et al., 2011; Inoue and Berg, 2017). This modelling approach is used for projections to potential future climate scenarios in order to evaluate the impact of climate change on refugial areas for riparian species (D'Amen et al., 2011), the future distribution of invasive species in comparison to native riparian species (Ikeda et al., 2014) or to predict changes in functional connectivity among populations along a river (Inoue and Berg, 2017). Coupling SDM with dispersal vectors allows to get more realistic information on the future distribution of species under climate change impact (e.g. see Alarcon et al., 2015; Engler and Guisan, 2009; Travis et al., 2013) and can be applied e.g. for landscape planning.

In this study, we use SDM and add information on dispersal constraints and life history traits to gain insight in the future distribution of six species of the riparian plant community *Salicion elaeagni* (olive willow plant community) which is listed as endangered (Delarze et al., 2013; Delarze and Gonseth, 2015). We compared species which are characteristic for the habitat and which are highly dependent on river dynamics (*Myricaria germanica*, *Salix daphnoides*) with species that can also occur in secondary habitats such as human-made gravel pits (*Hippophaë rhamnoides*, *Salix elaeagnos*, *S. myrsinifolia*, *S. triandra*) and represent transitions to other habitat types (Ellenberg, 2010; Müller, 1955).

To gain insight into functional connectivity along river networks, we include information on species' dispersal abilities and on barriers to dispersal. The study focuses on three main questions: First, is the predicted future distribution of riparian plant species affected by climate change? Second, can SDM be used to gain knowledge on functional connectivity for both rare and widespread riparian plant species in Switzerland? Third, is the future distribution of species affected by barriers to dispersal? The applied modelling framework includes stepwise dispersal to simulate the spread of riparian species in Switzerland based on species' presence, current and future climate conditions as well as geological and topographic habitat characteristics.

2. Methods

2.1. Study species

This study focuses on characteristic plant species of the endangered riparian plant community *Salicion elaeagni.* Each species has a unique distribution pattern and a different conservation status in Switzerland: *Hippophaë rhamnoides* is a dioecious, wind-pollinated shrub native throughout Europe, which is common in South-Eastern Switzerland, but vulnerable and even endangered in North-Western regions of Switzerland (Lauber et al., 2014). *Myricaria germanica* is a shrub native to Eurasia, vulnerable throughout Switzerland (Bornand et al., 2016), and even locally extinct in North-Western Switzerland (Lauber et al., 2014). *Salix daphnoides* is a up to 10 m high tree, mainly occurring in floodplain areas linked to rivers in Central Europe (Lauber et al., 2014). It is common in the South of Switzerland, but nearly threatened (Northern Switzerland) and even highly endangered in other regions (North-Western Switzerland). *Salix elaeagnos* is a native shrub (which can grow up to 16 m) to Central and Southern Europe and common in floodplains in Switzerland (Lauber et al., 2014). *Salix myrsinifolia* is a up to 5 m high shrub native to Europe and Siberia, and common throughout Switzerland (Lauber et al., 2014). *Salix triandra* is a shrub native to Europe and common in Switzerland, although its current distribution is mainly in the North-Western part of Switzerland (Lauber et al., 2014).

2.2. Niche modelling

Presence data for Switzerland for the study species were retrieved from the Swiss National data base Info Flora (request date October, 01, 2015, www.infoflora.ch, for information on study species see Appendix, Methods). Only coordinates with a precision of $\leq$100 m and collection dates 1960 until 2015 were used. This long time span was necessary to obtain sufficient number of presence points for robust modelling (Fourcade et al., 2014). Data cleaning included duplicate removal and maintenance of only one coordinate point per grid cell (100 × 100 m) to avoid spatial autocorrelation (Guisan and Zimmermann, 2000).

We applied the maximum entropy modelling technique using the software maxent for each species individually (Phillips et al., 2006). Environmental predictor layers for Switzerland with a resolution of 100 × 100 m were chosen according to species' ecology and previous findings for plant species (see in Breiner et al., 2015; Camathias et al., 2013). After excluding collinear layers ($>$ 0.75, Pearson correlation test in raster package in R, Hijmans and van Etten, 2012), nine layers of climatic, topographic and geological predictors were applied for model calibration: mean annual temperature, mean annual precipitation (observed meteorological data from 1960 to 2013, data sourced by the Federal Office of Meteorology and Climatology MeteoSwiss, data prepared by the division of Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, following the methodology used in Thornton et al., 1997), wetness index (following Tarboton, 1997, see in Camathias et al., 2013), nutrient-holding capacity, northness, slope, soil permeability, hydrometric properties (long-term water retention in the soil) and water-holding capacity (for details see Camathias et al., 2013). All layers were clipped in ArcGIS (ESRI, 2015), using a buffer of 1000 m around all rivers in Switzerland (based on maps with a scale of 1:2500, see in Baumgartner, 2009) to restrict modelling of habitat suitability to riparian areas along rivers. The extensive buffer around rivers allows for the inclusion of all riparian areas

as well as 10 independent re-sampling procedures of 10,000 background points for the modelling (see Phillips et al., 2009).

The performance of the models were assessed by the area under the curve (AUC) of the receiver operating characteristics (see Phillips et al., 2006). We used the mean of the AUC of the ten-fold-crossvalidation to evaluate the predictive power of the model for each species independently (Hirzel et al., 2006). Additionally, the models were evaluated using Boyce index as calculated by the ecospat package in R using a sliding window (Hirzel et al., 2006). This index is suitable for presence-only models and does not depend on background points as sampled by the software maxent (Hirzel et al., 2006). Additionally, the Spearman correlation between the ratio of predicted to expected species presences and habitat suitability was calculated and visualized using the R package ecospat (Hirzel et al., 2006).

The calibrated model for each species was projected to eight time intervals in the future (2014–2023, 2024–2033, 2034–2043, 2044–2053, 2054–2063, 2064–2073, 2074–2083, 2084–2093) by adjusting the climate data (temperature and precipitation) as predicted by two regional climate scenarios based on $CMIP_5$ (ICCP Fifth Assessment, 2009). The first of two scenarios for change is the regional climatic scenario CLMcom-CCLM4-8-17 calculated and downscaled from the global climatic scenario CNRM-CERFACS-CNRM-CM5 using emission predictions of 4.5. The second scenario is the regional climatic scenario CLMcom-CCLM4-8-17 calculated and downscaled from the global climatic scenario ICHEC-EC-EARTH by ICHEC using emission predictions of 8.5. Information of both climate scenarios were obtained from the coordinating body of CORDEX (see http://wcrp-cordex.ipsl.jussieu.fr and http://www.euro-cordex.net). The original climate data as provided by CORDEX has previously been downscaled on a 100 × 100 m grid over Switzerland using the Delta change method, and using measured data on temperature and precipitation as an independent reference (observed meteorological data from 1961 to 1990, data sourced by the Federal Office of Meteorology and Climatology MeteoSwiss, data prepared by the division of Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, following the methodology used in Thornton et al., 1997). Calculated differences in temperature and precipitation based on the reference period revealed that the first scenario represents a moderate climate change with moderately increasing temperature, and constant precipitation in summer which only moderately increases in winter (*moderate climate change*, compare to Appendix, Fig. A.1). Contrary to that, the second scenario predicted a comparably dry summer and extreme temperature increase compared to other methods for prediction and therefore represents a more extreme climate change scenario than the first scenario (*extreme climate change,* compare to Appendix, Fig. A.2).

To account for competition for land use along rivers, we further modified every habitat suitability map of each species for each time period (nine maps per species and climate change scenario, see above) as obtained by the software maxent. Maps were adjusted to be in accordance with Swiss regulations on minimal spatial requirements for the riverine zone (waters protection ordinance, status as of February 2, 2016). By this law, small rivers up to 2 m wide should occupy a total area of 11 m while intermediate rivers of 2–15 m require a zone of 2.5 times the size of the river bed and additional 7 m buffer. Rivers with a river bed > 15 m require individually determined riverine zones. River bed size information was obtained from a file on river morphology from the Federal Office for the Environment (Baumgartner, 2009). We added a buffer of 5.5 m on each side to rivers up to 2 m and a buffer of 22.5 m on each side to rivers of 2–15 m river bed size. The remaining rivers with bed sizes ranging from 15.1 m to 901 m were treated as follows: 15.1–50 m: 50 m buffer on each side; 50.1–100 m: 100 m buffer on each side; 100.1–200 m: 150 m buffer on each side; 200.1–300 m: 200 m buffer on each side; 300.1–400 m: 250 m buffer on each side; 400.1–500 m: 300 m buffer on each side; 500.1–600 m: 350 m buffer on each side; 600.1–700 m: 400 m buffer on each side; 700.1–800 m: 450 m buffer on each side; and 800.1–901 m: 500 m buffer on each side. All habitat suitability maps were clipped with this buffer file before being used as input file for the dispersal analyses (see below), to take into account the limited space availability for the formation of riparian habitats. Starting with a reference situation (1960–2013), habitat suitability maps were updated eight times during the dispersal simulation for each climate change scenario.

2.3. Dispersal simulation

To simulate the maximal spread of species from the current to future suitable habitat, we used the MigClim package (Engler et al., 2012) in R (R Core Team, 2016). Dispersal kernels describe the probability of seed dispersal from a source population (current presence points of species) to neighboring cells of a 100 m × 100 m grid in this study (see Engler, 2012). The probability to colonize neighboring cells depends on the joint probability as obtained by the habitat suitability as well as the probability to disperse, which is usually derived from dispersal kernels, and limited by life history traits such as initial maturity age and age dependent propagule production (see Engler, 2012).

For *H. rhamnoides*, pollen is only dispersed over short distances and limits dispersal abilities of the species (Tian et al., 2004), but bird- and wind mediated dispersal as well as floating of fruits have been reported (for details see Appendix, Methods). We thus concluded, that the probability to reach the next cell 100 m apart from the source would be 1 in our simulation framework. To account for bird-mediated short distance seed dispersal, we included dispersal from 200 m to 1000 m with a constant probability of 0.01 to the dispersal vector (see Table A.1). Dispersal parameters for wind- and water-dispersed *M. germanica* were chosen according to results from trapping experiments and the modelling of the corresponding polynomic dispersal kernel for wind (see Table A.1). To account for intermediate distance dispersal by wind and water (e.g. by seasonal floods), we extrapolated the findings of the polynomic model to 300 m distance from the source shrub. Seed dispersal for *Salix* species and the corresponding wind dispersal kernels were obtained from a transect trapping study, following a negative exponential model (see Table A.1, following Gage and Cooper, 2005). We applied the negative exponential model to a maximum distance of 300 m.

For all species, rare long-distance dispersal was included from the end distance of the dispersal kernel (300 m and 1000 m respectively) to 10 km with a probability of 0.01 (for details see Appendix, Methods). Still, stochastic events such as e.g. extreme floods or habitat erosion were not included in the model. Life history traits such as initial maturity age and age dependent propagule production allow for a realistic simulation of seed dispersal and have been included in the simulation framework (see Appendix, Methods). Actual species presence points were implemented as mature samples, as information on the age of individuals was not available from the database.

The simulation of the spread of each species was predicted under different scenarios. For each species, we simulated a reference situation and subsequently analyzed the spread influenced by the two different climate change scenarios and limited by barriers to dispersal. We included the coordinates of different existing barrier types to

Table 1
Numbers of different barrier types along rivers in Switzerland.

Barrier type	Number of barriers
Sediment check dam	3512
Weir	1065
Dam	115
Tyrolean weir	95
Gate	93
Sill ≥70 cm height	50504
Spillway ≥70 cm height	104

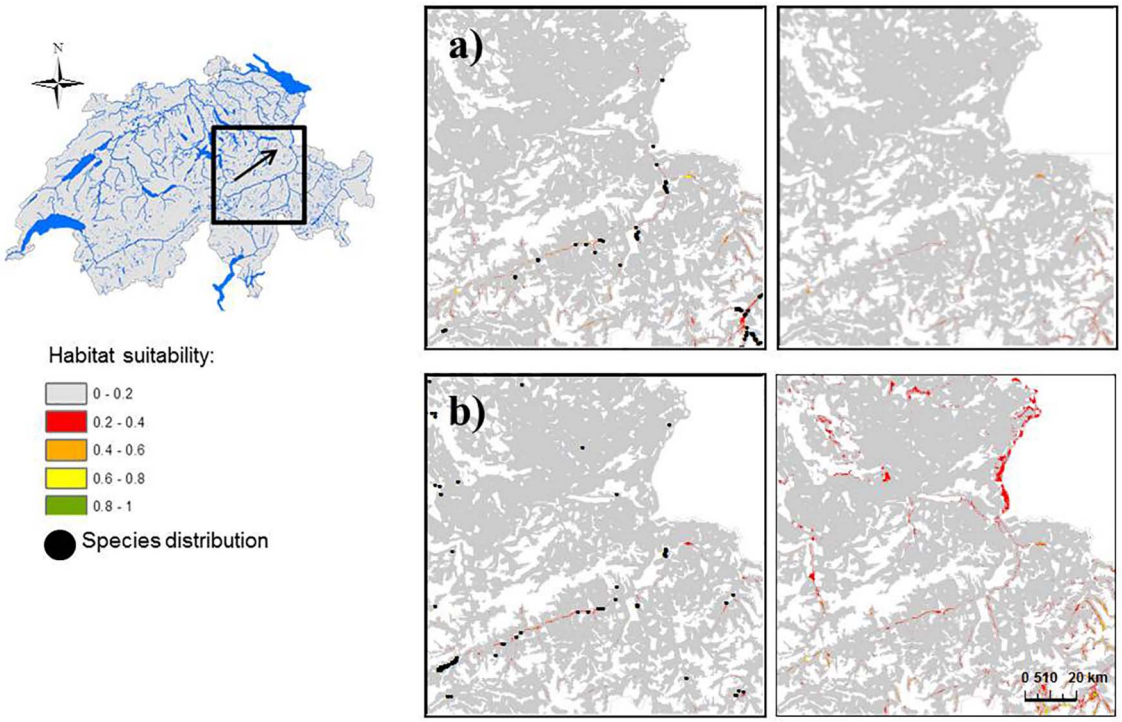

Fig. 1. Habitat suitability maps with details of river Rhine (flow direction shown with black arrow) for the two species with narrow ecological niche. The reference time span (1960–2013) is shown on the left and the projection to the very last time point in the simulation (2084–2093) assuming the extreme climate change scenario (based on ICHEC-EC-EARTH) is shown on the right. The two species *M. germanica* (a) and *S. daphnoides* (b) show few suitable habitats along the river Rhine both for the reference period as well as under the extreme climate change scenario.

dispersal (sediment check dams, weirs, dams, Tyrolean weirs and gates, see Table 1, data from Baumgartner, 2009) to the MigClim package applied. Spillways and sills were both included as barriers if the height exceeded 0.7 m, as this height is considered to have an impact on the permeability of the riverway (Göggel and Wagner, 2006). The locations of the barriers were transformed to represent barrier cells in a raster file, and a restrictive barrier setting was applied, where crossing from a source cell to a sink cell is not possible when at least one path leading from source to sink is inhibited by a barrier cell ("strong" barrier type, see Engler, 2012). This setting was equal for all barrier types.

We simulated the potential distribution of the species after dispersal limited by all barriers, dispersal limited by just major barriers (all barriers without sills and spillways) as well as dispersal to suitable habitat without barriers under both climate change scenarios using the package MigClim (Engler et al., 2012). For each species, barrier scenario and climate model, we performed ten independent simulations. Comparisons between starting and future distributions of species, after 8 updates of suitability maps (corresponding to eighty years of dispersal total), both in the presence and absence of barriers to dispersal were compared using paired t-tests (Welch, 1947) in R (R Core Team, 2016). To assess the impact of climate change scenarios on species distribution, we simulated a reference situation with dispersal of species under different dispersal barrier scenarios but without adjusting habitat suitability maps for future climate scenarios. Comparisons between different climate change scenarios and barrier removal scenarios were calculated using t-tests (Welch, 1947) and repeated measure ANOVA in R (R Core Team, 2016). Repeated measure ANOVA was performed since simulations started with the same initial data points and where therefore not independent. Prior to all repeated measure ANOVA tests, both outlier detection by graphical representation (boxplots) and variance testing using the package stats were performed in R (R Core Team, 2016).

2.4. Connectivity analyses

The output of the dispersal simulations for each climate change scenario and each species independently was additionally used to analyze connectivity along rivers in Switzerland. We used information on the colonized and decolonized cells for each species. The turnover of a species during 80 years of dispersal simulation was calculated as the total cells colonized during the simulations without the cells which became decolonized (because the habitat becomes unsuitable, see Engler, 2012). Difference in turnover between barrier scenario and climate change scenario was compared using t-tests (Welch, 1947) and repeated measure ANOVA in R (R Core Team, 2016). Additionally, the number of decolonized cells were compared between species by repeated measure ANOVA in R (R Core Team, 2016).

3. Results

3.1. Niche modelling

Models estimated by maxent revealed generally high AUC values and small standard deviations (sd): *H. rhamnoides* 0.852 (sd 0.108), *M. germanica* 0.925 (sd 0.032), *S. daphnoides* 0.858 (sd 0.052), *S. elaeagnos* 0.769 (sd 0.0.042) and *S. triandra* 0.834 (sd 0.047). AUC > 0.75 indicate good prediction accuracy (compare to Manel et al., 2001). The only exception was the calibration model for *S. myrsinifolia* with an AUC of 0.635, indicating weak model precision. This led to the exclusion of this species from further analyses. Model evaluations showed generally high correlations between predicted to expected presence points and habitat suitability (Spearman correlation, 0.923–0.989, see also Figs. A.3–A.7).

Modelled habitat suitability varied considerably between species, with two species showing very few suitable habitats at all time intervals and under both climate change scenarios (the two species with the narrow niche, *M. germanica* and *S. daphnoides*, see Fig. A.8 for the

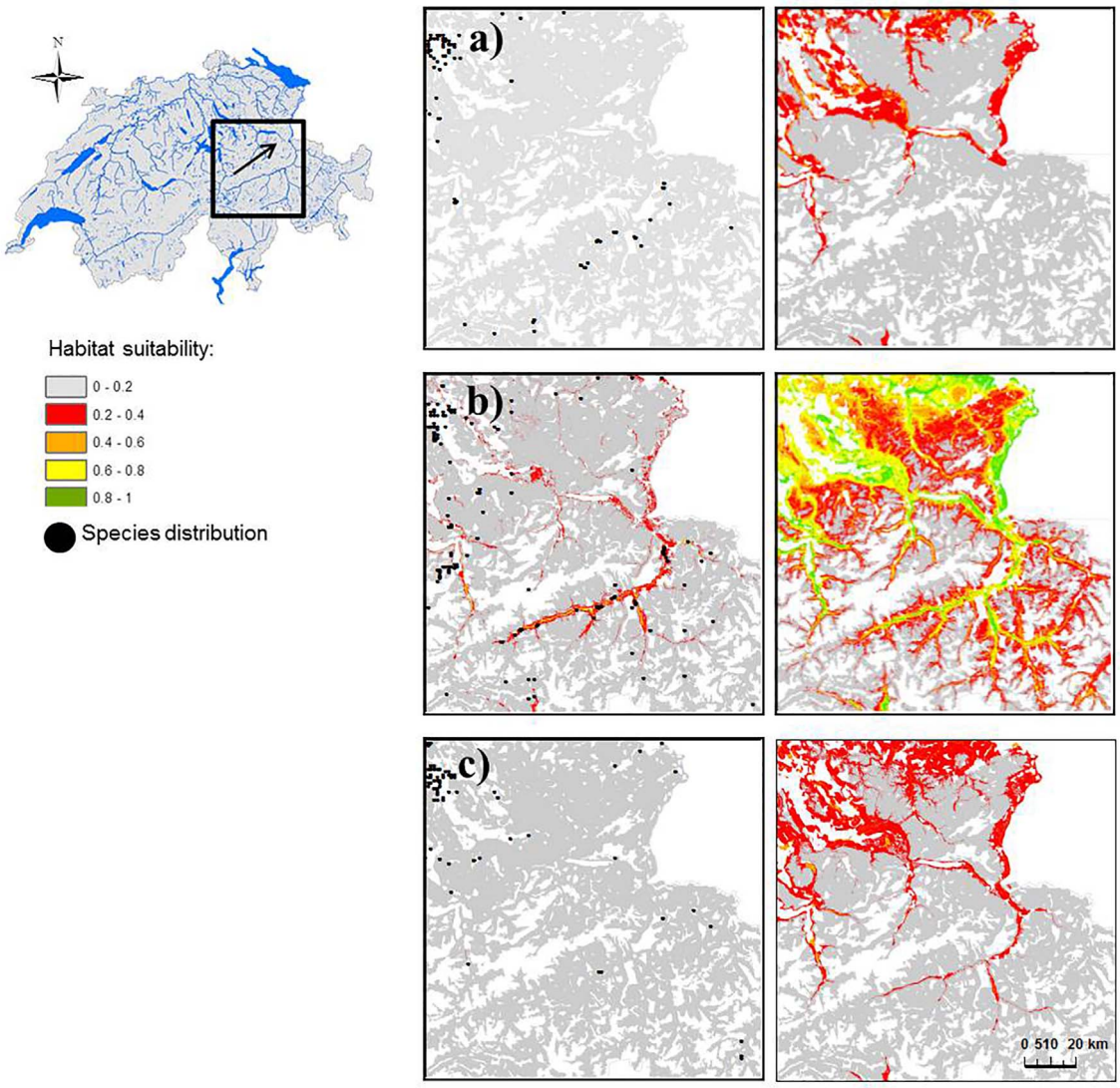

Fig. 2. Habitat suitability maps with details of river Rhine (flow direction shown with black arrow) for the three species with a broad ecological niche which can also occur in secondary habitat. The reference time span (1960–2013) is shown on the left and the projection to the very last time point in the simulation (2084–2093) assuming the extreme climate change scenario (based on ICHEC-EC-EARTH) is shown on the right. For all three species shown here, *H. rhamnoides* (a), *S. elaeagnos* (b) and *S. triandra* (c), more suitable habitats are predicted under the extreme climate change scenario compared to the reference situation.

Table 2
Overview of output of species distribution simulations under dispersal constraints and various climate change scenarios. Three different scenarios for the presence ("all barriers" and "major barriers") and absence ("no barriers") of barriers to dispersal for Switzerland were analyzed. Climate change scenarios include: Reference (observed climate 1960–2013, no future change), moderate climate change (moderate temperature increase) and extreme climate change (temperature increase and dryer summer, see text for details). Values shown in the upper part of the table are mean numbers of occupied cells over n = 10 independent simulations. Cells occupied at the beginning of the simulations ("initial") are shown in the first column. t-tests (below) show differences between initially occupied cells and occupied cells at the end of the simulation (2084–2093). All t-tests were significant ($p < 0.01$).

Barrier scenario		No barriers			Major barriers			All barriers		
Climate change scenario		Reference	Moderate	Extreme	Reference	Moderate	Extreme	Reference	Moderate	Extreme
Occupied cells	Initial									
H. rhamnoides	426	1226.4	584.9	1678.4	1213.3	587.9	1718.5	1182.5	575.5	1558.2
M. germanica	222	2159.8	1986.6	1993.7	2108.2	1954	1963.8	1960.3	1805.6	1797.6
S. daphnoides	241	1219.0	997.8	1012.7	1210.7	970.8	993.6	1167.6	941.3	957.4
S. elaeagnos	690	5355.6	3560.5	5005.6	5233.0	3506.8	4954.1	4898.6	3269.7	4576.2
S. triandra	284	1180.3	688.3	952.7	1159.8	684.3	891.9	1110.3	642.8	868.9
t-values of pairwise t-test initial occupied vs. simulated future occupied[*]										
H. rhamnoides		−88.065	−8.490	−46.522	−58.358	−12.184	−28.911	−54.020	−8.716	−31.400
M. germanica		−162.020	−119.200	−129.240	−122.450	−117.570	−188.410	−127.930	−96.930	−184.540
S. daphnoides		−104.790	−55.074	−100.910	−159.660	−59.366	−77.313	−115.140	−67.898	−74.082
S. elaeagnos		−234.250	−105.400	−176.310	−144.190	−119.030	−159.610	−173.400	−217.330	−102.750
S. triandra		−134.210	−35.811	−47.187	−86.381	−32.580	−40.260	−68.917	−34.612	−32.002

[*] $p < 0.01$ for all pairwise tests.

moderate future climate change scenario and Fig. A.9 for the extreme climate change scenario). Details from the modelled habitat suitability showing the river Rhine area indicate few suitable habitats both for the reference period as well as for the years 2084–2093 under the extreme climate change scenario for *M. germanica* and *S. daphnoides* (Fig. 1). For *H. rhamnoides, S. triandra* and *S. elaeagnos*, the species with a wider ecological niche, projections under both climate change scenarios predicted a shift and an increase in areas with high suitability (see Figs. A.8 and A.9, and details for the river Rhine in Fig. 2). This increase was especially strong for the prediction for the two willow species under the extreme climate change scenario (see Figs. A.8 and A.9).

3.2. Dispersal simulation

The potential distribution after simulated wind and water dispersal from the current presence points in whole Switzerland revealed significantly more newly occupied cells for all species analyzed, both for barrier and non-barrier limited dispersal (overall: initial to occupied cells, $t = -25.74$, $p < 0.001$; scenario without barrier: $t = -14.822$, $p < 0.001$; scenario with major barriers included: $t = -14.821$, $p < 0.001$; scenario with all barriers included: $t = -14.954$, $p < 0.001$). If species were tested separately, all showed significantly more occupied cells both in the presence and in the absence of barriers, when comparing initial occupied cells to cells occupied at the end of the dispersal simulation for each climate scenario separately (see Table 2). The simulation of the reference situation, assuming no climate change and no barriers to dispersal, showed up to a 10-fold increase of occupied cells for each species (Table 2). Boxplots for each species revealed no outliers in the total number of occupied cells at the end of 10 simulations and variance testing showed no significant difference in variances of colonized cells between species (all $p > 0.05$). Repeated measure ANOVA analysis revealed a significant influence of the climate change scenario used for simulation of the occupied cells (F: 205.4, $p < 0.001$). Less occupied cells were found for simulations under both climate change scenarios compared to the reference situation, with the exception of *H. rhamnoides*, which showed more occupied cells under the extreme climate change scenario (Table 2). For all species studied here, the simulation assuming an extreme climate change scenario resulted in more occupied cells than the simulation assuming a moderate climate change scenario, even if the spread was limited by major barriers or all barriers (Table 2). Only *M. germanica* revealed more occupied cells under moderate climate change than extreme climate change assumptions when all barriers were included in the simulation (Table 2). When comparing occupied cells at the end of simulations without barriers to simulations with barriers at the species level, t-tests generally revealed significant results (Table 3). When sills and spillways, which form the majority of barriers along rivers in Switzerland (Table 1), were excluded as barriers to dispersal (scenario "major barriers"), the strong effect of barriers got lost, and pairwise comparisons were mainly non-significant (Table 3).

3.3. Connectivity analyses

The number of colonized cells increased for all species (Table 4 and Fig. 3). Contrary to the findings for occupied cells, the colonized cells did not show the highest increase in the simulation of the reference situation (no climate change, no barriers) for all species (Table 4). *Myricaria germanica* and *S. daphnoides* both showed highest number of colonized cells under reference assumptions, while all other species studied here showed the highest colonization potential under the extreme climate change scenario (Table 4). Similar to the findings for occupied cells, the simulation including barriers to dispersal revealed a significant influence on colonized cells for all species and most climate scenarios, but the effect disappeared with the exclusion of sills and spillways (Table 3). The influence of barriers on colonization patterns of species can be visualized at the regional scale (Fig. 4).

The turnover of species based on colonized and decolonized cells was not significantly different when comparing simulations with all barriers to simulations without barriers for all climate scenarios (all species, reference: $t = 0.586$, $p = 0.56$; moderate climate change: $t = 0.584$, $p = 0.56$; extreme climate change: $t = 0.670$, $p = 0.50$, see also Table 4). Boxplots showed no outliers in turnover of cells at the end of 10 independent simulations per species, and variance testing revealed no significant difference in variances of turnovers between species (all $p > 0.05$). Repeated measure ANOVA analysis indicate as significant effect of the climate scenario on turnover of species (F: 205.4, $p < 0.001$). Decolonized cells were not significantly different between the two climate change scenarios ($t = -1.026$, $p = 0.306$), although the amount of decolonized cells was slightly lower under extreme climate change assumptions than under moderate climate change assumptions for all species and barrier scenarios (Table 4). No outliers were revealed in 10 independent simulations of decolonized cells per species, and variance testing showed no significant difference in variances between groups of species (all $p > 0.05$). Repeated measure ANOVA revealed significant differences of decolonized cells between species (F: 215.7, $p < 0.001$).

Table 3
Comparisons between occupied and colonized cells at the end of simulations applying different scenarios where barriers of dispersal were included or excluded. Significant t-values ($p < 0.05$) are indicated in bold. Simulation without barriers ("no barriers") are compared to simulations of dispersal limited by all barriers ("all barriers") and to simulations limiting dispersal by barriers without sills and spillways ("major barriers", for details see text). Climate change scenarios include: Reference (observed climate 1960–2013, no future change), moderate climate change (moderate temperature increase) and extreme climate change (temperature increase and dryer summer, see text for details).

Climate change scenario	All barriers vs. no barriers			Major barriers vs. no barriers		
	Reference	Moderate	Extreme	Reference	Moderate	Extreme
Occupied cells						
H. rhamnoides	**−2.749**	−0.373	**−2.673**	−0.805	0.132	0.770
M. germanica	**−11.076**	**−8.212**	**−12.147**	**−2.697**	−1.561	−1.809
S. daphnoides	**−4.739**	**−3.308**	**−4.501**	−0.745	−1.478	−1.557
S. elaeagnos	**−14.842**	**−9.815**	**−9.538**	−3.289	−1.493	−1.424
S. triandra	**−5.319**	**−2.981**	**−3.630**	−1.689	−0.242	**−2.950**
Colonized cells						
H. rhamnoides	**−2.630**	−0.194	**−2.706**	−0.805	0.146	0.770
M. germanica	**−11.021**	**−8.092**	**−12.069**	**−2.646**	−1.526	−1.732
S. daphnoides	**−4.171**	**−3.336**	**−4.338**	−0.745	−1.551	−1.557
S. elaeagnos	**−14.555**	**−9.752**	**−9.449**	**−3.289**	−1.499	−1.424
S. triandra	**−5.100**	**−2.850**	**−3.543**	−1.688	−0.242	**−2.950**

Table 4
Turnover of cells during simulation of dispersal under various climate change scenarios. The reference condition reflects simulations without temperature and precipitation adjustments ("reference") in contrast to simulations under two climate change scenarios ("moderate" and "extreme"), where changes influencing habitat suitability are included (for details see text). Number of colonized cells and decolonized cells are shown in the presence ("all barriers" and "major barriers") and absence ("no barriers") of barriers. Values shown are mean over n = 10 independent simulations.

Barrier scenario		No barriers			Major barriers			All barriers		
Cells	Inital	Colonized	Decolonized	Turnover*	Colonized	Decolonized	Turnover	Colonized	Decolonized	Turnover
Reference situation, no change										
H. rhamnoides	426	800.4	–	800.4	787.3	–	787.3	756.5	–	756.5
M. germanica	222	1937.8	–	1937.8	1886.2	–	1886.2	1738.3	–	1738.3
S. daphnoides	241	978.0	–	978.0	969.7	–	969.7	926.6	–	926.6
S. elaeagnos	690	4665.6	–	4665.6	4543.0	–	4543.0	4208.6	–	4208.6
S. triandra	284	896.3	–	896.3	875.8	–	875.8	826.3	–	826.3
Moderate climate change										
H. rhamnoides	426	608.5	451.6	156.9	611.8	451.9	159.9	603.5	454	149.5
M. germanica	222	1887	123.4	1763.6	1854.9	122.9	1732	1707.4	123.8	1583.6
S. daphnoides	241	938.1	188.3	749.8	909.9	187.1	722.8	881.6	181.3	700.3
S. elaeagnos	690	3513.9	652.4	2861.5	3460.5	652.7	2807.8	3224.7	645	2579.7
S. triandra	284	665.3	264	401.3	661.3	264	397.3	621.8	263	358.8
Extreme climate change										
H. rhamnoides	426	1652.3	401.9	1250.4	1692.4	401.9	1290.5	1530.7	398.5	1132.2
M. germanica	222	1893.1	122.4	1770.7	1864.5	122.7	1741.8	1698.2	122.6	1575.6
S. daphnoides	241	944.7	180.0	764.7	925.6	180.0	745.6	891.4	175.0	716.4
S. elaeagnos	690	4909.6	603.0	4306.6	4858.1	603.0	4255.1	4484.2	598.0	3886.2
S. triandra	284	929.7	264.0	665.7	868.9	264.0	604.9	847.9	263.0	584.9

* Turnover: colonized cells − decolonized cells.

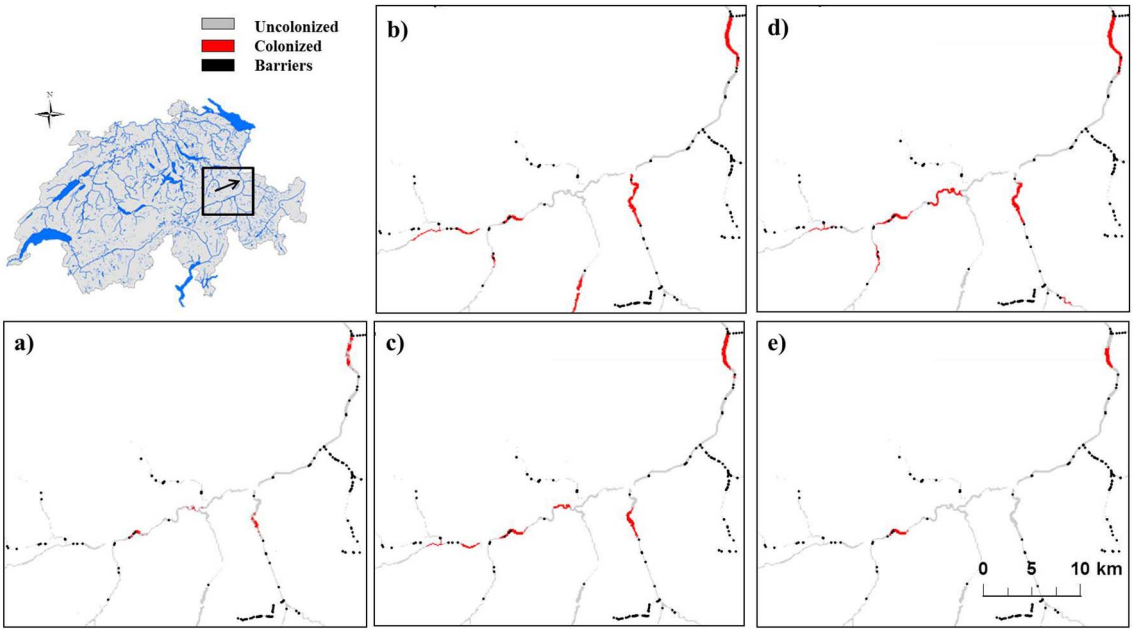

Fig. 3. Colonized cells after dispersal simulation along a stretch of river Rhine (flow direction shown with black arrow) in the presence of barriers (black dots). The predicted occupied cells as well as the cells colonized during simulations are shown for each species (for simplicity, both are shown in red). The habitat suitability maps used for simulations are assuming the extreme climate change scenario (based on ICHEC-EC-EARTH). Maps are details of the simulation output over whole Switzerland. Species: a) *H. rhamnoides* b) *M. germanica,* c) *S. daphnoides,* d) *S. elaeagnos,* e) *S. triandra.*

4. Discussion

4.1. Predicted future distribution of riparian species

In this study, we present a species based coupled modelling framework with dispersal simulations to predict the future distribution of riparian species, allowing to target conservation decisions in floodplains. Although the species investigated in this study are all linked to the *Salicion elaeagni* plant community, the modelled habitat suitability for the species revealed highly diverse areas of predicted suitable current and future habitats. This depends on the different ecological niches of the species considered, which is broader for *H. rhamnoides, S. elaeagnos* and *S. triandra* compared to the very narrow niche and the dependence on river dynamics for *M. germanica* and *S. daphnoides* (Ellenberg, 2010). Assignments of riparian species to plant communities are inconsistent due to various successional stages (compare Delarze et al., 2013; Ellenberg, 2010; Moor, 1958). Despite individual differences in predicted habitat suitability, all species showed dramatic changes in potentially available habitat in the future, similar to findings for willow (*Salix* ssp.) and tamarisk (*Tamarix* ssp.) species in North America (Ikeda et al., 2014).

The number of occupied cells after dispersal simulation from current

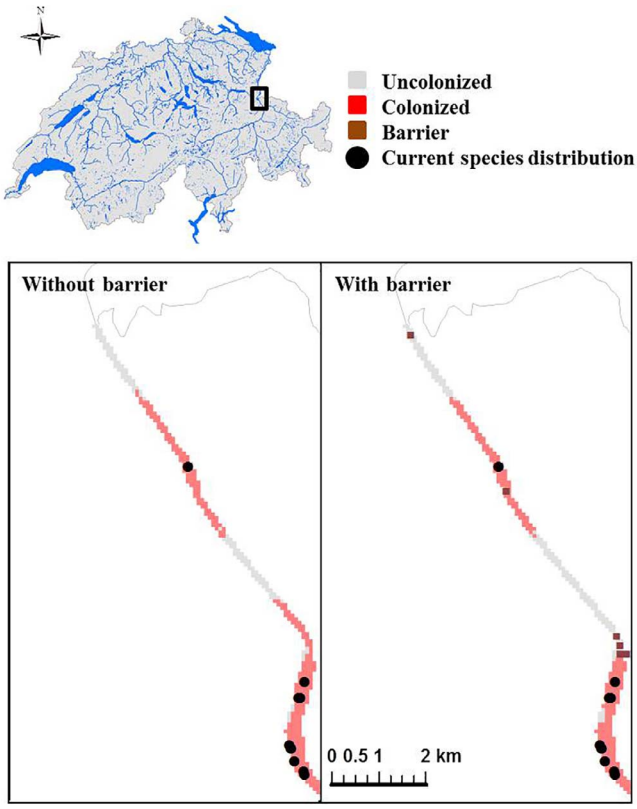

Fig. 4. Maps of a short stretch of the river Rhine for *M. germanica* contrasting simulations with barriers and without barriers. The predicted occupied cells as well as the cells colonized during simulations are shown for each species (for simplicity, both are shown in red). The habitat suitability maps used for simulation are assuming the moderate climate change scenario (based on CNRM-CERFECS-CNRM-CM5). Maps are details of the simulation output over whole Switzerland. Without barriers (left), the species is expanding northwards further than under dispersal constraint by barriers (right). One barrier was crossed by rare long distance events (shown on the right), allowing for the spread of the species southward (right).

species presence points to suitable habitat was significantly different between climate change scenarios. Additionally, the ability to spread varied considerably among species: Surprisingly, not the species with the forecasted highest proportion of suitable habitats (*H. rhamnoides, S. elaeagnos* and *S. triandra*) showed the highest increase of occupied cells. Instead, *M. germanica,* with relatively few suitable habitats, showed a 10-fold increase in presence points of the species after 80 years of dispersal (compare to Table 2). This can be explained by the low numbers of decolonized cells found for *M. germanica* (Table 4). The number of simulated occupied cells was not predictable by factors such as total initial presence points, generation time or dispersal ability, as the comparison of the three willow species showed. *Salix daphnoides* and *S. triandra* had comparable total initial presence points as well as similar life history and dispersal traits. Still, dispersal simulations resulted in highly diverse future distribution patterns (see Fig. 3), since the habitat suitability maps as well as the initial distribution of each species were different (see Figs.1 and 2). Our coupled modelling approach therefore revealed the importance to study interactions between climate change, dispersal and life history traits when predicting the future distribution of a species (similar to findings for tree species, see Meier et al., 2012).

Habitat loss is an important factor to be considered when planning future areas for restoration and species conservation, as riparian habitats in general and the habitat for the plant community *Salicion elaeagni* in particular, are small already (Delarze et al., 2013; Delarze and Gonseth, 2015). In our study, habitat loss due to climate change was inferred from the number of decolonized cells, which varied significantly between species, but was very similar between the two climate change scenarios. This pattern suggests that the present points might thus more likely reflect the past ecological history of the species (Ruete et al., 2014), and not the future habitat of the species. This finding highlights the importance of functional connectivity along river networks, as the loss of single populations due to climate change was frequent for riparian species in this study (see Table 4).

4.2. Functional connectivity of riparian species

Functional connectivity from current species' distribution to potential future habitat was assessed in our simulation approach. Dispersal parameters as well as life history traits (e.g. age to first maturity) influence the spread of a species (Demars et al., 2014), although dispersal distances are frequently used as a proxy for connectivity of habitats (Clobert et al., 2012). Seed dispersal distances estimated by wind dispersal experiments are limited for the riparian species studied here (Fink et al., 2017; Gage and Cooper, 2005). Contrary to that, bird-dispersed seeds are transported over larger distances (Viana et al., 2013), therefore increasing connectivity. Our simulations showed that the bird-dispersed *H. rhamnoides* did not colonize and occupy more cells than the wind-dispersed species (Fig. 3, Table 2). Despite assuming similar dispersal abilities for three willow species (*S. daphnoides*, *S. elaeagnos*, *S. triandra*), they were not equally successful to spread from source populations (Tables 2 and 4), due to differing habitat suitability maps (compare to Figs.1 and 2). Therefore, the dispersal distances *per se* are not sufficient to assess functional connectivity and to forecast to the future distributions of a species.

Connectivity of riparian habitats is especially important, as single populations may decline or go extinct due to extreme floods, extreme droughts or habitat loss due to e.g. sediment dynamics (Ellenberg, 2010; Naiman et al., 2005). The turnover of a species, estimated as the difference between colonized and decolonized cells during the simulation process, gives an indication on the species' colonization potential. For *S. triandra,* the turnover was low, while other species showed high colonization potential (*M. germanica, S. elaeagnos*), and in the case of *H. rhamnoides*, the potential was highly dependent on the chosen climate scenario. Our simulations for the turnover confirmed the ecological observation for riparian species and their colonization potential: e.g. *M. germanica* is considered to be a very successful first colonizer of gravel banks (Moor, 1958). The species composition of this habitat varies according to the age of the habitat (Ellenberg, 2010; Moor, 1958; Naiman et al., 2005). Habitats at a later successional stage (after eight to ten years) are mainly dominated by *H. rhamnoides* and *S. elaeagnos* (Moor, 1958), which are late colonizers, but grow older (Ellenberg, 2010). As our simulation approach took into account life history traits and habitat parameters, the spatially explicit information of the species' spread can be used to plan restoration areas along rivers in the real world. The method also allows to identify areas, where 'stepping-stone' habitats are needed, because current or future potential habitats are not connected. These structural elements provide sufficient space for the intermittent survival of small populations, and they are crucial to link larger populations or metapopulations, if space for riparian habitats is limited (Freckleton and Watkinson, 2002).

4.3. Barriers to dispersal along rivers

Barriers to dispersal along river corridors had a negative impact on both colonized cells as well as occupied cells simulated for the plant species of the *Salicion elaeagni* community. Different barriers resulting in decreased gene flow have been reported from genetic data for the German tamarisk (Werth et al., 2014), and dams are known to considerably change dispersal patterns (Brown and Chenoweth, 2008; Goodson et al., 2003; Jansson et al., 2005). Excluding barriers such as sills and spillways as barriers to dispersal in our simulation approach did not reveal a congruent pattern for all species (see Table 3), and the effect of the barriers was mainly diminished. This finding can be

explained by limited dispersal abilities which lead to an underestimation of the effect of barriers (Fink et al., 2017; Gage and Cooper, 2005). Additionally, given the different demographic histories of individual species, some can occur directly upstream and downstream of certain barrier types as e.g. sills and spillways, which generally show less height difference upstream and downstream than large barriers (Allan, 2007). Dams might even alter habitat upstream to provide new habitat for riparian species (Sitzia et al., 2016). Nevertheless, our scenario including all barriers across rivers is likely still underestimating all potential barriers to seed dispersal. Future studies need to identify more barriers to dispersal for single species (e.g. non-natural river dynamics in stretches of rivers, dams alongside rivers preventing seeds to be transported or landing on suitable habitat), to be included in a more refined future simulation framework (McRae et al., 2012).

The influence of barriers on predicted species distribution can be visualized for individual species (see Fig. 4). Therefore, the simulation framework can be used as a planning tool and visually show the effect of barrier removal along river catchments (Reichert et al., 2007). This can help to investigate the potential of the species to spread along certain river stretches, thereby allowing to adjust expectations for success control of restorations (Darby and Sear, 2008). This is of importance as space availability is limited and other conflicting interests such as e.g. hydropower production need to be considered (Darby and Sear, 2008). Removal of barriers has a strong effect on seed dispersal (Engstrom et al., 2009), and selective dam removal or measures to enhance connectivity (e.g. bypass-tunnels) need to be considered (Caplat et al., 2016). Our approach allows to include this data for subsequent analyses, and could also be applied to other organisms, e.g. insects.

4.4. Modelling limitations

Our study included all river networks in whole Switzerland. Management decisions are usually taken at the local scale (Darby and Sear, 2008). To choose the right scale for a modelling approach is challenging (Elith and Leathwick, 2009; Guisan et al., 2013). The modelling procedure itself should include a large area to sufficiently reflect the species occurrence range (Elith and Leathwick, 2009). For Switzerland, biogeographic regions with different ecological conditions are an ideal scale to cover the whole variability of habitats where the species modelled could occur (Wohlgemuth, 1996). As data availability in Switzerland allowed to consider a good resolution of 100 m, the output of the modelling framework can also be used to gain information on potential possible distribution at a smaller scale (e.g. river stretch, compare to Figs. 3 and 4). We avoided modelling at the catchment scale, as species presence data might be highly influenced by catchment-specific river alterations and land use along rivers (Sitzia et al., 2016).

Our modelling approach includes environmental parameters, which are independent of human management. The outcome of the SDM approach strongly depends on prior data availability and predictor choice (Elith and Leathwick, 2009; Guisan et al., 2013; Hijmans and Elith, 2014). Similarly, forecasting to future time points including various future climate change scenarios is accompanied by uncertainties and high differences between climate change scenarios (see in Araujo et al., 2005). To gain a comprehensive insight for e.g. success control of river restorations and for conservation planning for a species, we propose to include information on river dynamics (e.g. channel dynamics, see Richards et al., 2002). Predictors dependent on human activity like e.g. information on infrastructure, land cover and management can be included in future models, once the information is available for future predictions. Additionally, the effect of sediments, a habitat key structure for riparian plant species, has to be investigated, in relation to seed dispersal by water (Carthey et al., 2016; Groves, 2010; Groves et al., 2009).

5. Conclusion

This study shows that both climate change and barriers along rivers have a significant effect on the future distribution of riparian plant species. Therefore, neither dispersal abilities of sessile plant species *per se* nor the presences of a single barrier alone can be used to predict the future occurrence of species along a river. As climate change scenarios additionally induce habitat loss as indicated by the high amount of decolonized cells, the current areas with species presence are not persistent across time. This highlights the importance of studying functional connectivity for plant species dependent on dynamic riparian habitats. Our results show that some regions are more likely to allow for the spread of a species, while for other areas, there is limited connectivity of potential future habitats. Due to limited space availability along rivers in Switzerland, conservation of vulnerable species of the *Salicion elaeagni* plant community needs to focus on providing 'stepping-stone' habitats. The current approach allows to identify potentially suitable areas for such habitat patches along river networks. 'Stepping-stones' will ensure the re-colonization of restored areas as well as gene flow between populations of a species.

Glossary

- *Species distribution models (SDM):* Modelled prediction of the current or future distribution of species based on occurrence (presence) data and environmental predictor layers.
- *Functional connectivity:* The actual movement of individuals and the exchange of genes (gene flow) between populations.
- *Stepping stone habitat:* Habitats providing sufficient space for the temporal survival of small populations, linking larger populations or metapopulations.

Acknowledgements

Dirk Schmatz provided information on future climatic data and the figures representing temperature and precipitation anomalies. We are grateful to Lyudmyla Dymytrova, Klaus Ecker and Martin Hägeli for help with ArcGIS layers. We acknowledge the World Climate Research Program's Working Group on Regional Climate, and the Working Group on Coupled Modelling, former coordinating body of CORDEX and responsible panel for CMIP5 and the climate modelling groups for producing and making available their model output. The Swiss data base for plants, www.infoflora.ch, provided information on species occurrence. Funding was provided by the Swiss Federal Offices for the Environment for the project "habitat and sediment dynamics".

Appendix A. Methods

Life history traits

The precise initial maturity age is not known for all studied species. Still, for *H. rhamnoides*, generation times of 5 years have been reported (Bartish et al., 2006; Jia et al., 2012). For a *Myricaria* species, flowering after one year has been reported (*M. laxiflora*, Chen and Xie, 2007). Still, other studies suggest maturity at 2–3 years for *M. germanica* (Bill et al., 1997; Lener et al., 2013), and we thus set the age to 3. For *Salix* ssp., maturity age was set to 6 years, estimated by growth (see in Ellenberg, 2010). Initial maturity of 10 years as assumed in a study with *S. viminalis* and *S. schwerinii* (Fogelqvist et al., 2015) seems unlikely for *Salix* ssp. as investigated in this study, as quick spread and reproduction for willows has been

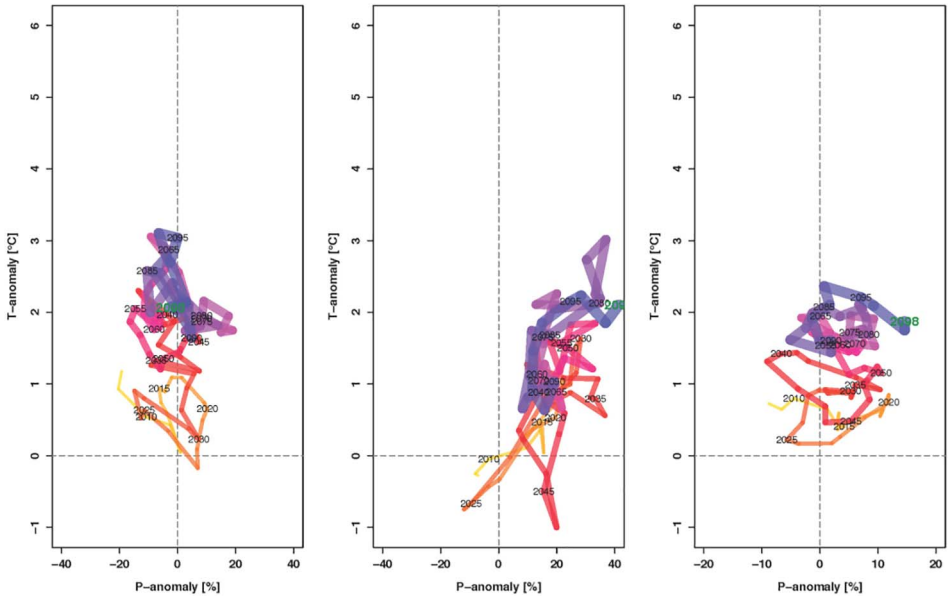

Fig. A.1. Temperature and precipitation anomalies of the "moderate future climate scenario", the regional climatic scenario CLMcom-CCLM4-8-17 calculated and downscaled from the global climatic scenario CNRM-CERFACS-CNRM-CM5 using emission predictions of 4.5. For each year in the future as well as its summer (June, July and August) and its winter (January, February, December) months, the mean was compared to the mean of the observed data for the reference period 1961–1990 (data sourced by the Federal Office of Meteorology and Climatology MeteoSwiss, data prepared by the division of Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, following the methodology used in Thornton et al., 1997). The anomalies were calculated as absolute anomalies for temperature (in °C) and relative anomalies (in %) for precipitation. All results have been averaged over whole Switzerland and been smoothened with a 5-year sliding mean. The colors range from light yellow (near future) to dark purple (far future). Temperature shows a moderate increase (right side) while precipitation increases mainly during winter (middle). Figure courtesy of Dirk Schmatz, division of Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL.

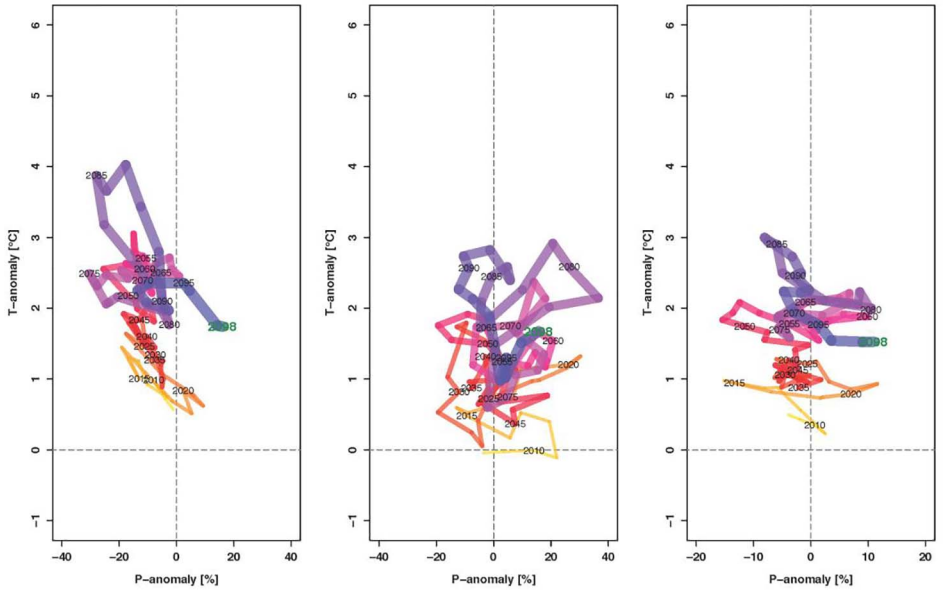

Fig. A.2. Temperature and precipitation anomalies of the "extreme future climate scenario", the regional climatic scenario CLMcom-CCLM4-8-17 calculated and downscaled from the global climatic scenario ICHEC-EC-EARTH by ICHEC using emission predictions of 8.5. For each year in the future as well as its summer (June, July and August) and its winter (January, February, December) months, the mean was compared to the mean of the observed data for the reference period 1961–1990 (data sourced by the Federal Office of Meteorology and Climatology MeteoSwiss, data prepared by the division of Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, following the methodology used in Thornton et al., 1997). The anomalies were calculated as absolute anomalies for temperature (in °C) and relative anomalies (in %) for precipitation. All results have been averaged over whole Switzerland and been smoothened with a 5-year sliding mean. The colors range from light yellow (near future) to dark purple (far future). Temperature shows a stronger increase than the moderate scenario (all figures, compare to Fig. A.1), while precipitation decreases during summer (left side). Figure courtesy of Dirk Schmatz, division of Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL.

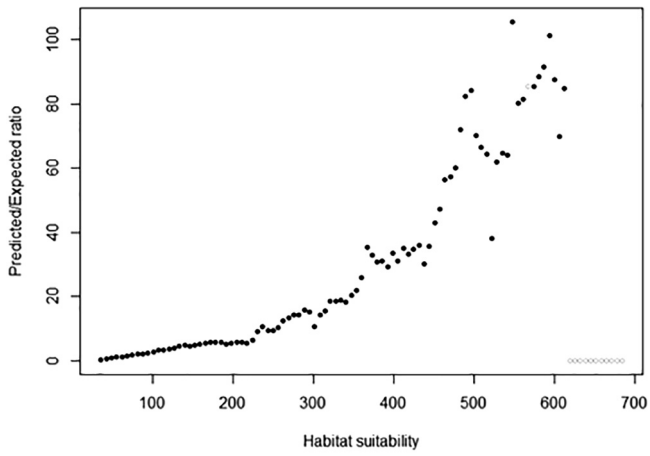

Fig. A.3. Ratio of predicted/expected species presence related to the habitat suitability obtained by the maximum entropy model for *H. rhamnoides*.

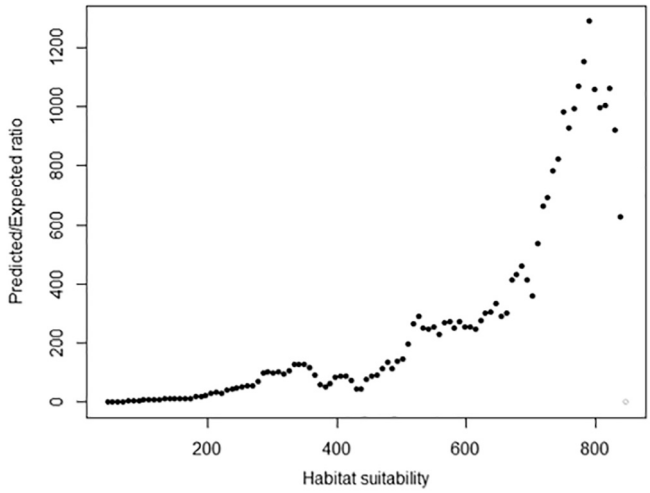

Fig. A.4. Ratio of predicted/expected species presence related to the habitat suitability obtained by the maximum entropy model for *M. germanica*.

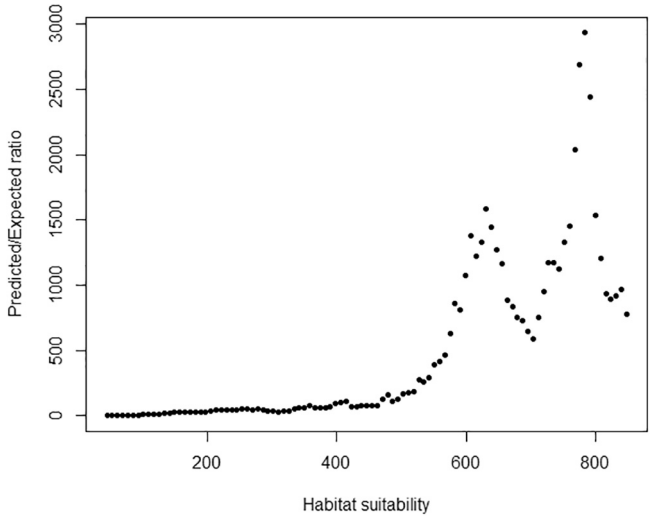

Fig. A.5. Ratio of predicted/expected species presence related to the habitat suitability obtained by the maximum entropy model for *S. daphnoides*.

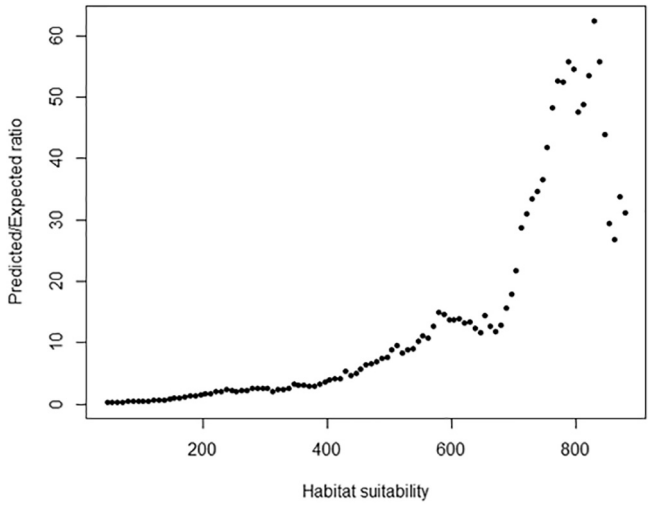

Fig. A.6. Ratio of predicted/expected species presence related to the habitat suitability obtained by the maximum entropy model for *S. elaeagnos*.

reported for this habitat type (Moor, 1958).

For the vector parameter propagule production (Engler, 2012), no information on the difference in propagule production after maturity age was found for the species investigated. Still, previous findings for *M. germanica* suggest, that older individuals are likely to produce more seeds than younger plants (Lanz and Stecher, 2009). We thus use information on different age structure for *M. germanica, Hippophae* ssp. and *S. purpurea* and

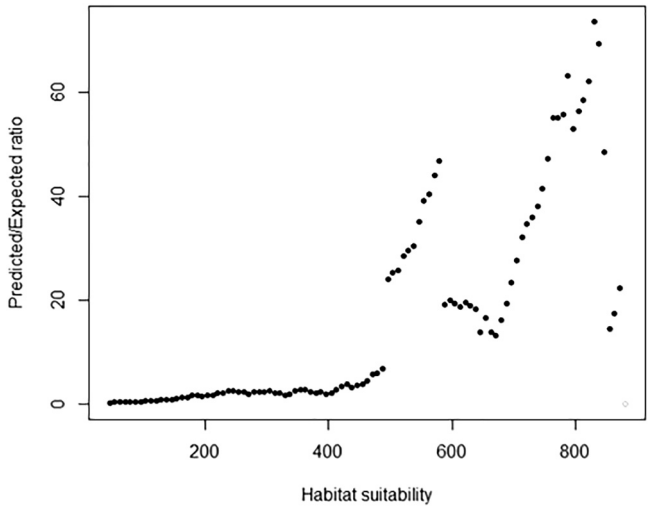

Fig. A.7. Ratio of predicted/expected species presence related to the habitat suitability obtained by the maximum entropy model for *S. triandra*.

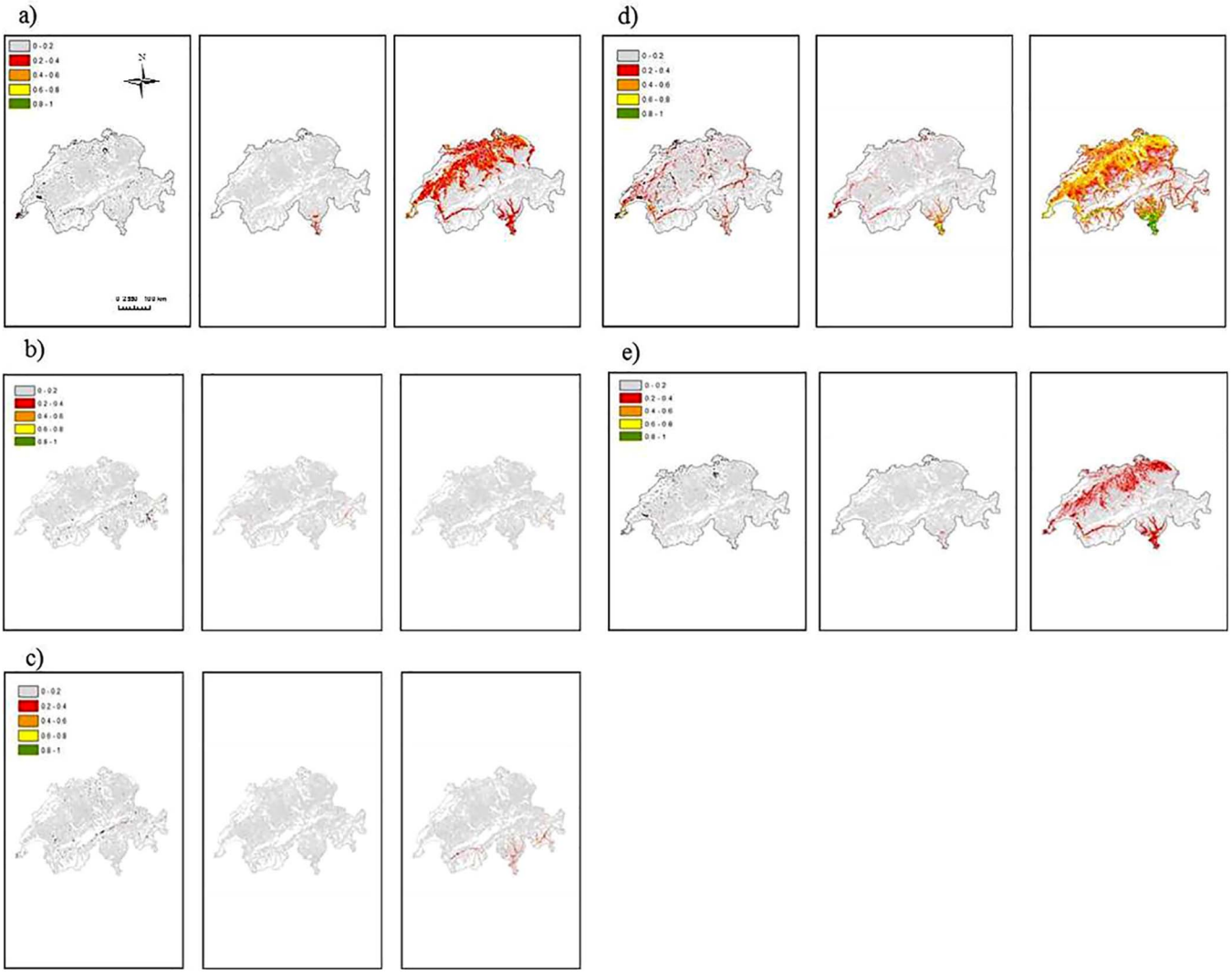

Fig. A.8. Habitat suitability maps of five riparian species based on topographic, geological and climatic predictors (calibration period 1960–2013, left side) and future climatic layers based on predictions for 2044–2053 (middle) and 2084–2093 (right side). The data used for the forecasting was based on the regional climatic scenario CLMcom-CCLM4-8-17 was calculated and downscaled from the global climatic scenario CNRM-CERFACS-CNRM-CM5 (method described in Thornton et al., 1997) using emission predictions of 4.5.This model represents a moderate climate change with moderately increasing temperature (see http://wcrp-cordex.ipsl.jussieu.fr and http://www.euro-cordex.net), and constant precipitation in summer which only moderately increases in winter month (*moderate climate change*). a) *H. rhamnoides,* b) *M. germanica*, c) *S. daphnoides*, d) *S. elaeagnos*, e) *S. triandra*. Black circles represent species occurrences (presence points) included in the model.

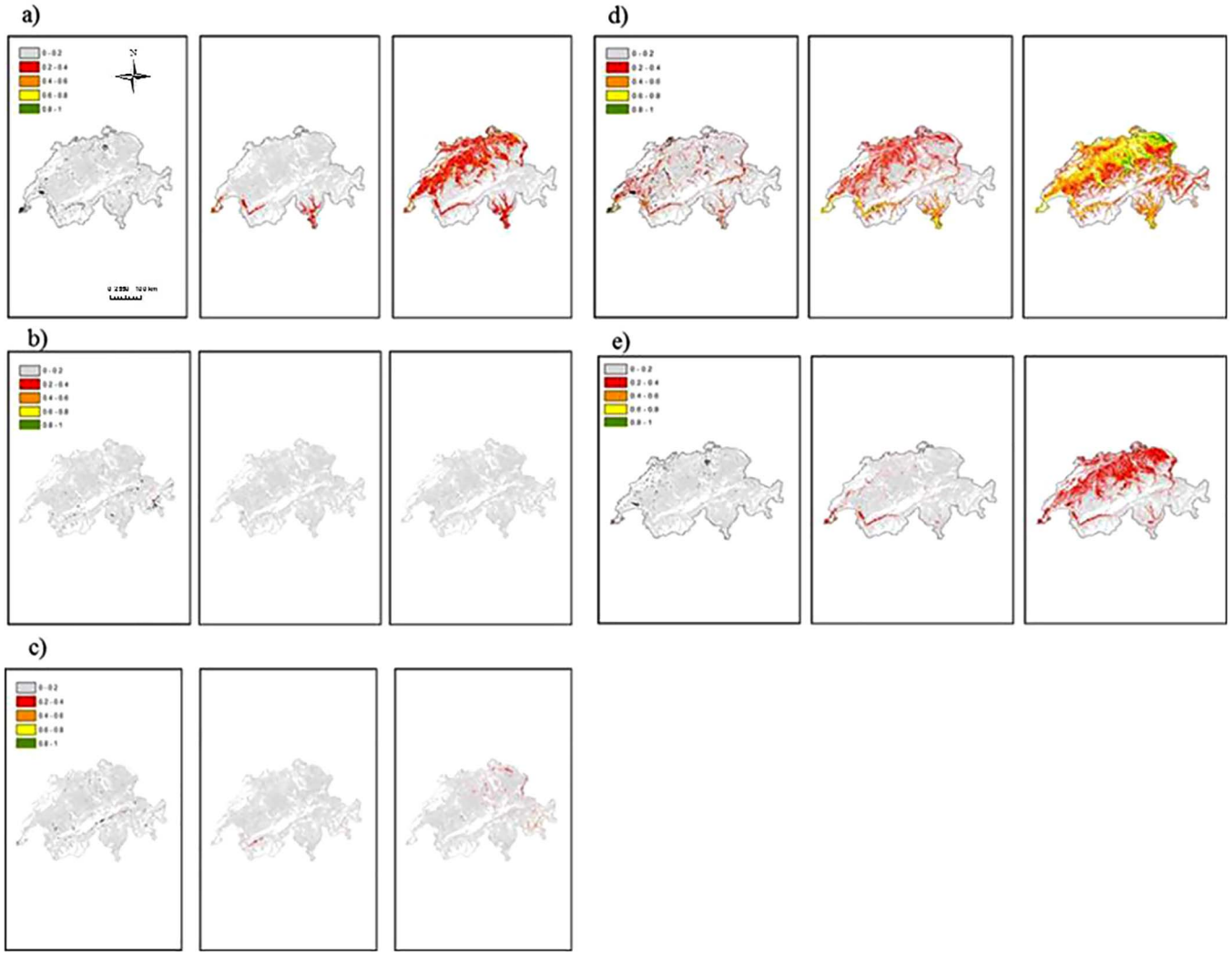

Fig. A.9. Habitat suitability maps of five riparian species based on topographic, geological and climatic predictors (calibration period 1960–2013, left side) and future climatic layers based on predictions for 2044–2053 (middle) and 2084–2093 (right side). The data used for the forecasting was based on the regional climatic scenario CLMcom-CCLM4-8-17, which was calculated and downscaled from the global climatic scenario ICHEC-EC-EARTH (method described in Thornton et al., 1997) using emission predictions of 8.5. This model predicts a comparably dry summer and extreme temperature increase compared to other methods for prediction (see http://wcrp-cordex.ipsl.jussieu.fr and http://www.euro-cordex.net) and therefore represents a more extreme climate change scenario than the first scenario (*extreme climate change*). a) *H. rhamnoides*, b) *M. germanica*, c) *S. daphnoides*, d) *S. elaeagnos*, e) *S. triandra*. Black circles represent species occurrences (presence points) included in the model.

assume linear curves for the relationship between seed production and time until peak growth (see in Ellenberg, 2010; Moor, 1958): *M. germanica* reaches peak growth after 10 years, and is not likely to live longer as an individual (Ellenberg, 2010). We thus set an increase for propagule production to a vector of (0.33, 0.66, 1) for a propagule increase of 30% between age of maturity (3 year) and age of full maturity (5 year). For *H. rhamnoides,* the peak in growth is reached after 20 years (Ellenberg, 2010), and we thus use a vector of 17% increase (0.17, 0.33, 0.5, 0.67, 0.83, 1) between 5 years (maturity) and 10 years (full maturity). For *S. purpurea,* the peak height was reported after 25 years (Ellenberg, 2010), and we thus used a vector with an increase of 10% in propagule production for *Salix* ssp. from the age of maturity of 6 years to 15 years (full maturity). We do not take into account the disappearance of species by succession (see in Ellenberg, 2010; Moor, 1958), as the majority of all seeds per species fall next to the mother tree (Gage and Cooper, 2005; Lanz and Stecher, 2009; Tian et al., 2004), and individuals are thus likely to be replaced by juvenile plants of their species (Bill et al., 1997).

Seed dispersal

While plants are generally assumed to be dispersed by wind over short distances (Willson, 1993), riparian species are frequently dispersed by multiple vectors such as wind, water and animals (Nilsson et al., 1991). Unfortunately, field experiments (trapping, release of marked seeds etc.) tackle each dispersal vector independently (e.g. see in Bullock and Clarke, 2000; Nilsson et al., 1991; Tackenberg, 2003). Dispersal kernels as applied in the MigClim package (Engler et al., 2012) describe the probability of seed dispersal from a source population (current presence points of species) to neighboring cells of a 100 m × 100 m grid in this study (see in Engler, 2012). We use kernels based on trapping experiments for short-distance wind-dispersal and of information on bird-mediated dispersal for *H. rhamnoides*. Additionally, dispersal by rare extreme events such as strong winds and rare, extreme flooding are included as randomly and independently generated dispersal events and are not affected by barriers (see in Engler, 2012).

For *H. rhamnoides*, bird-mediated dispersal of fruits over 250 m (Bolibok et al., 2009) up to several kilometers (Lu et al., 2006) has been reported.

Table A.1
Dispersal kernels of riparian species.

Name	Name Model	Formula	Parameters	Dispersal vector in MigClim	Reference
M. germanica	Polynomic	ax^b	a = 3616.7, b = −1.175	c(0.8511, 0.0972, 0.0516)	Lanz and Stecher (2009)
H. rhamnoides	Uniform distribution	a	a = 0.01	c(1.0, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1)	Adapted from description after Tian et al. (2004)
Salix ssp.	Negative exponential	$a + be^{-cx}$	a = −49.53, b = 52, c = 0.0002	c(0.9008, 0.0376, 0.0616)	Gage and Cooper (2005)

Bird-mediated dispersal kernels are usually best fitted to inverse power or negative exponential kernels (Clark et al., 2005). Lack of isolation by distance in genetic data (Sun et al., 2006; Tian et al., 2004) and germination experiments of bird dispersed seeds show successful long distance dispersal (Lu et al., 2006). Additionally, wind dispersal of dried fruits has been suggested (see in Li and Beveridge, 2003; Müller, 1955). Several studies report that fruits of sea buckthorn can drift over ground and into water, and are then considered to float to the shore (Ellenberg, 2010; Müller, 1955; Pijl, 1969).

Exact seed dispersal estimates e.g. by trapping experiments of wind dispersed seeds are still missing. Bird-mediated dispersal kernels are usually best fitted to inverse power of negative exponential kernels (Clark et al., 2005). Still, as *H. rhamnoides* is a dioceous plant and thus dependent on cross-pollination for seed production, we used information on wind dispersal of pollen as a proxy for wind-mediated seed dispersal in our simulation focusing on connectivity. 60–90% of all pollen of *H. rhamnoides* ssp. *sinensis* were trapped in 12 m distance from the source tree, and not more than 20 m of dispersal was reported (Tian et al., 2004). We thus concluded, that the probability to reach the next cell 100 m apart from the source would be 1 in our simulation framework. To include the probability of bird-mediated short distance seed dispersal, we included dispersal from 200 m to 1000 m with a constant probability of 0.01 to the dispersal vector.

For *M. germanica*, both upstream and downstream migration over several kilometers have been detected by genetic analyses (Werth and Scheidegger, 2014), similar to findings of another *Myricaria* species (*M. laxiflora*, Chen and Xie, 2007). The small, pappus-bearing seeds of the German Tamarisk are suitable for wind dispersal (Bill et al., 1997; Endress, 1975). Floating of seeds and germination of seeds after time spend under water was successful (Bill et al., 1999; Lanz and Stecher, 2009). Dispersal parameters for *M. germanica* were chosen according to results from trapping experiments and the modelling of the corresponding polynomic dispersal kernel for wind (see Table A.1). To account for intermediate distance dispersal by wind and water (e.g. by seasonal floods), we extrapolated the findings of the polynomic model to 300 m distance from the source shrub.

While a difference in timing of seed dispersal between willow species has been reported (Sakio and Tamura, 2008), dispersal mechanisms and distances are still very similar between species (e.g. see in Gage and Cooper, 2005). Seeds are mainly dispersed by wind (Chmelar and Meusel, 1979; Ellenberg, 2010; Gage and Cooper, 2005), but seeds have also been collected after drifting through water (Bill et al., 1999). Seed dispersal for *Salix* species and the corresponding wind dispersal kernels were obtained from a transect trapping study, following a negative exponential model (see Table A.1, following Gage and Cooper, 2005). We applied the negative exponential model to a maximum distance of 300 m.

Probabilities of seed dispersal from the presence points to cells of 100 m length were calculated by the area under the distribution kernel density curve. Long-distance dispersal was also included with similar probabilities for all species. As long-distance dispersal is usually hard to observe, estimates are thus frequently inferred in trapping or seed marking experiments (but see in Herrmann et al., 2016). For all species, rare long-distance dispersal was included from the end distance of the dispersal kernel (300 m and 1000 m respectively) to 10 km. Although longer maximal dispersal distances obtained from e.g. genetic data for both upstream and downstream dispersal have been reported for some of the study species (e.g. *M. germanica*, see in Wubs et al., 2016), these findings might represent various time scales of dispersal movements (contemporary and historic gene flow). We choose a maximum dispersal distance represented in the time span under investigation (10 years between each environmental change). Similarly, we assigned a probability of 1% to long distance dispersal events to account for rare events by strong winds and extreme floods returning every 100-years (compare to definitions in Herrmann et al., 2016).

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